Root dynamics in bottomland hardwood forests of the Southeastern United States Coastal Plain

Marianne K. Burke[1,3] & Jim L. Chambers[2]

[1] *USDA Forest Service, Southern Research Station, Center for Forested Wetlands Research, 2730 Savannah Highway, Charleston, SC 29414, USA.* [2] *School of Renewable Natural Resources, Louisiana Agricultural Experiment Station, Louisiana State University Agricultural Center, Baton Rouge, LA, 70803, USA.* [3] *Corresponding author**

Abstract

Effects of flooding on root dynamics appear nonlinear and therefore difficult to predict, leading to disparate and often contradictory reports of flooding impacts on production in bottomland hardwood forests. We explored root dynamics in two adjacent wetland habitats by comparing results obtained from several methods of estimating root processes. Also, we tested the influence of flooding on root dynamics of cherrybark, overcup, water and swamp chestnut oaks. Fine root biomass in the laurel oak habitat was greater ($\alpha < 0.05$) than in the swamp tupelo habitat (5.7 vs. 2.4 Mg ha^{-1}), as was fine root necromass (2.4 vs. 1.3 Mg ha^{-1}), productivity (2.3 vs. 0.3 Mg ha^{-1} yr^{-1} when the sum of significant increments method was used, 5.6 vs. 2.5 Mg ha^{-1} yr^{-1} when the maximum minus minimum method was used, and 1.2 vs. 1.0 Mg ha^{-1} yr^{-1}, when the root screen method was used), and turnover (40% and 12% per year). Mortality estimates were lower in the laurel oak habitat (1.3 and 1.2 Mg ha^{-1} yr^{-1}) than in the swamp tupelo community (2.8 and 2.1 Mg ha^{-1} yr^{-1}) when significant increment and maximum minus minimum methods were used, respectively. This apparent contradiction between estimates of production and mortality may be due to more rapid decomposition rates in the more aerated soil of the laurel oak than in the swamp tupelo forest type. Roots in the swamp tupelo habitat appeared to be longer-lived than in the laurel oak habitat. We concluded that there was greater investment in roots in the laurel oak habitat, where a shallow rooting zone and episodes of flooding and drought required drastic changes in root structure and physiology. In contrast, the swamp tupelo habitat had a deeper rooting zone and more consistently moist to flooded hydroperiod, allowing flood adapted roots to persist. The four oak species varied in their phenology of root production and response to flooding, from no difference among treatments for overcup oak to dramatic reductions in root growth during and after flooding for cherrybark oak. Flooding enhanced or at least did not negatively influence root growth in overcup oak, but seriously impacted root growth and survival of cherrybark oak and swamp chestnut oak. Different responses were attributed to the timing of root production: root growth began early for cherrybark oak so spring flooding severely affected this species. Growth in overcup oak began later and ended earlier than the other species tested, allowing the species a means of avoiding flood stress.

Introduction

Root production is not necessarily equal or even proportional to aboveground production (Megonigal and Day, 1992), being more greatly impacted by flooding than is shoot production (Burke et al., 2000b; Day and Megonigal, 1993; Jones et al., 1996; Megonigal and Day, 1992; Powell and Day, 1991) Also, the relationships between root dimensions and longevity that were identified for terrestrial trees do not apply in wetlands (Eissenstat et al., 2000). As a result, effects of flooding

* FAX No: 843-766-8734.
  E-mail: mburke@fs.fed.us

on root dynamics are nonlinear and difficult to predict, contributing to the disparate and contradictory reports of flooding effects on production in bottomland forests (Broadfoot, 1967; Hall and Smith, 1955; Harms et al., 1980; Hosner and Boyce, 1962).

In general, process-level studies tend to be more challenging in flooded than on drained sites. There is an inherent difficulty of operating in a variable and changing water table, and there is not yet a consensus on the best methods for quantifying root dynamics even in terrestrial habitats (Kurz and Kimmons, 1987; Lauenroth et al., 1986; Singh et al., 1984; Vogt et al., 1986). Probably the most accurate estimates of root dynamics come from comparisons of results obtained using a variety of the numerous established methods. All existing methods have both strengths and weaknesses, and because so many different methods have been used to estimate root production and turnover, only when several methods are employed on a site are we able to accurately compare results among studies (Vogt et al., 1998).

In this study, we quantified root dynamics in two bottomland hardwood forest types using several common methods. Also, to help explain differences in root dynamics between the forest types, we tested the influence of flooding on four endemic oak species: cherrybark oak (*Quercus pagodaeifolia* Raf.), swamp chestnut oak (*Q. michauxii* Nutt.), water oak (*Q. nigra* L.), and overcup oak (*Q. lyrata* Walt.). These oaks were found in the forest types studied here and in slightly more elevated surrounding forest stands, and the species were chosen to identify a range of life history strategies related to flood tolerance.

Methods

Ecosystem study site

A study was conducted in the floodplain of the Coosawhatchie River, a fourth-order, anastamosing, blackwater river with a drainage area of approximately 1000 km². The study site is owned by MeadWestvaco Corporation and is located in Jasper County near Point South, South Carolina USA (80° 58′ W, 32°39′ N). Rainfall averages 123 cm yr^{-1}, temperature averages 10 °C, and the growing season is 246 days (Stuck, 1980). The floodplain is approximately 1.6 km wide and surface relief ranges about 2 m.

Five main forest types were identified in a previous study (Burke et al., 2000a) and the root dynamics of two adjacent types were contrasted in this study. The swamp tupelo (*Nyssa sylvatica* var. *biflora* (Walter) Sargent) forest type contained from 9 to 25% of the basal area in water tupelo (*Nyssa aquatica* L.), swamp tupelo, and baldcypress (*Taxodium distichum* (L.) Rich.), < 15% of the basal area was in laurel oak (*Quercus laurifolia* Michaux), sweetgum (*Liquidambar styraciflua* L.) and red maple (*Acer rubrum* L.). The laurel oak forest type had >15% of the basal area in laurel oak and also contained water oak (*Quercus nigra* L.), sweetgum, red maple, water tupelo and swamp tupelo (Burke et al., 2000a). Dominant trees were more than 75 years old (personal communication, John Martin, MeadWestvaco Corporation).

Soils in the laurel oak type were classified in the Brookman and Rutledge series (Murray et al., 2000). The Brookman series is a fine, mixed, thermic, Typic Umbraqualf, with thick, black, loamy surface layers and dark gray clayey subsoils. The Rutledge series is a sandy, siliceous, thermic Typic Humaquepts, devoid of leached E and argillic B horizons, underlain by very dark grayish-brown and gray loamy fine sand that is frequently ponded (Miller, 1971). The Brookman series was typically vegetated by the swamp tupelo community, although the soils underlying some of this community was in the Nakina series, a fine-loamy, siliceous, thermic, Typic Umbraqualf, similar to the Brookman but with more shallow (50 cm) surface layers of black loam. Significant differences between soils included more clay in the swamp tupelo habitat and more sand in the laurel oak habitat (Burke et al., 2000a).

Soils were typical of blackwater river floodplains in that they were acidic, had high percent soil organic matter, a low proportion of clay, and a higher proportion of sand than was previously reported for alluvial rivers (Burke et al., 2000a). However, soils at this site were more acidic, had higher soil N and P availability and clay content, and lower soil silt content than generally found in descriptions of blackwater river floodplains (Wharton et al., 1982). Bulk densities in the B-horizons were higher than has been previously reported, indicating rooting volumes may be limited (Burke, unpublished data). Sedimentation rates were low (Hupp and Schening, 2000), and flood events were numerous, short in duration, and sometimes occurred during the growing season (personal observation). Elevation within the swamp tupelo habitat averaged 4.4 m and ranged from 4.3 to 4.6 m above sea level for the laurel oak habitat.

Hydrologic characterization

Hydroperiod was characterized by monitoring ground- and surface-water level with continuously recording water level recorders (four wells and one river stage) and 18 observation wells. Regression analyses were performed using water-table elevations at the observation wells (dependent variable), and the five continuous recording wells and river stage. Models were produced (Eisenbies and Hughes, 2000), and those with the best fit were used to estimate hydroperiod for the two forest types for a year prior to and during the field study (1 October 1994 to 30 September 1997).

Root production

In each of the two forest types, a 300 m transect was delineated and marked at 20 m intervals. Samples were collected at each interval marker, after which each reference marker was moved 2 m farther along the transect to become the marker for the subsequent sampling date. Soil cores were collected at 15 cm depth intervals using a 10 cm diameter core bit attached to a rotating gasoline driven power-head. Samples were collected in 1996 on 1–4 April, 3–4 June, 29–30 July, 1–2 October, 2–3 December 1996, and 11–12 March, and 22–23 July, 1997. Soil was sampled to 60 cm in April 1996 and to 45 cm on subsequent dates.

Soil cores were stored at 4 °C until they were processed, usually within four weeks of collection. Sediment and non-root material was washed from root cores using a hydropneumatic root washer (Gillison's Variety Fabrication, Inc., Benzonia, MI). Washed root material was cleaned by hand and sorted into size classes and live and dead categories. Root diameter size classes were < 1 mm, 1- ≤3 mm, and > 3 mm. Vigor was based on friability and cortex integrity according to methods of McClaugherty et al., (1982) and Burke and Raynal (1994). Quality control involved reprocessing random samples and developing 'correction factors' to account for the bias of each sample processor. Roots were dried to a constant mass at 70 °C in a forced air-drying oven. Biomass and necromass estimates were means of values for all sample dates.

On May 3, 1996, a 200 m transect was established parallel to the sequential core transect in each community type. At each two m interval along these transects, a fiberglass screen (2 mm mesh, 5 cm wide, and 21 cm long) was inserted at a 45° angle to a vertical soil depth of 15 cm. Each of the 100 screens per habitat was randomly oriented with relation to aspect.

From each habitat, 15 randomly selected screens were removed on 10 July 1996, 10 September 1996, and 22 July 1997. Screens were extracted along with surrounding soil monoliths and were refrigerated intact within plastic bags at 4 °C until they were processed, usually within four weeks. Because productivity estimates for this method were to be calculated using root intersections and biomass conversion equations, and because root production, surface area, and physiology varies as a function of root diameter class (Vogt et al., 1989), each intersecting root was tallied according to diameter size class (<0.3 mm, 0.3–0.5 mm, >0.5–1.0 mm, >1.0–2.0 mm). Production was estimated based on a relationship between the length of roots in a cube of soil and the number of intersections between roots and a grid (Melhuish and Lang, 1968, 1971). This relationship was explained in detail by Baker et al., (2001). Fine root length production was estimated for 1 m^2 by 15 cm deep volume of soil by multiplying root length (cm) by 150 000. Root surface area (root length times π times root diameter = surface area) was estimated for each root diameter class for July 1997, assuming roots were cylinders of average diameter for each size class.

Fine root biomass production was estimated using three methods, and mortality was estimated using two methods. The 'Significant Increment' method of Edwards and Harris (1977) and McClaugherty et al., (1982) added the significant ($\alpha < 0.05$) increments in biomass or necromass based on 't'-tests to estimate production or mortality, respectively. The maximum minus minimum method (e.g. Burke and Raynal, 1994) estimated production and mortality as the difference between the maximum and minimum biomass (or necromass). The root screen method (e.g. Baker et al., 2001) was used to estimate biomass production and employed biomass conversion equations for four root diameter size classes in each forest type. Fine root turnover was estimated as annual root production/root biomass, based on the sum of significant increments method of estimating production.

Seedling study

Four oak species endemic to bottomland hardwood forests in the South Atlantic Coastal Plain were used to test effects of flooding on root dynamics: cherrybark oak , swamp chestnut oak, water oak , and overcup oak . Two experiments were conducted in 1992 at the Louisiana State University School of Forestry, Wildlife, and Fisheries Stress-House facility: a seedling
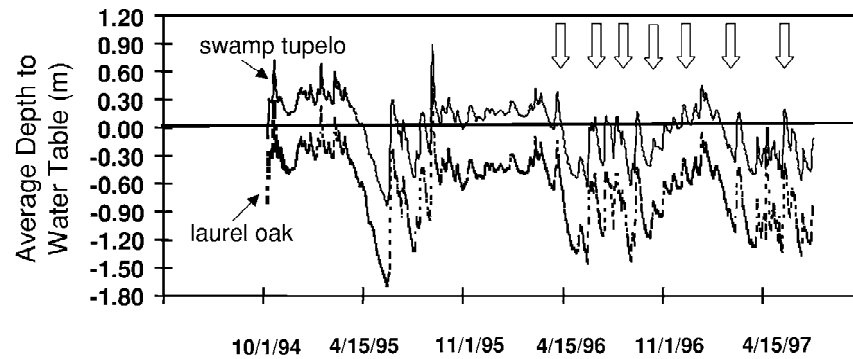
Figure 1. Hydrograph for the laurel oak and swamp tupelo habitats on the Coosawhatchie Bottomland Ecosystem Study site. Data were produced using models created with regressions performed on water table elevations at four observation wells in each community (dependent variable) and river stage and four continuous recording wells (independent variable). Vertical arrows show when soil cores were collected for root biomass estimation.

growth experiment (SGE) and a root growth experiment (RGE). All seedlings were germinated from seed and transplanted to PVC pots filled with Terra-Green, a sintered-clay potting medium (Oil Dri Corporation of America, Chicago Illinois), when they reached a height of 10 cm.

The PVC pots for the SGE were 8 cm diameter by 41 cm long. The bottom of each was covered with Monodure nylon (NMO-125 micron weave, Industrial Fabrics Corp., Minneapolis, MN) to prevent root egress from containers while permitting unimpeded water movement in and out of each pot. PVC pots for the RGE were constructed from 10 cm diameter by 41 cm length PVC pipes slit in half lengthwise. The open side of each RGE pot was covered with flat polycarbonate panels cemented in place. The bottom end of each pot was covered with the Monodure nylon as above.

Within each flood tank in the Stress House, containment walls were constructed to form flood treatment sections. Raised racks were placed in the bottom of each treatment section to facilitate pot drainage when not flooded. To simulate flooded conditions, tanks were filled with deionized water to a depth of 8–10 cm above the pot surface and 10–12 cm above the soil surface. Overhead irrigation maintained water levels in the flood treatments, irrigated control plots, and provide similar environments across treatments. Water levels were maintained by adding or removing water as needed.

The SGE used a split-plot design where whole plots were treatments (four replicates) and split plots were species. To simulate different lengths of seasonal flooding, flood treatments were (1) flooded from 15

October to 1 May, (2) flooded from 1 October to 1 June, and (3) a well-watered, unflooded control. There were 27 seedlings of each species per block in each treatment. Each group of seedlings for an individual species was placed together within a treatment block to reduce shading effects caused by inherent species growth differences. However, the position of a species group within each treatment block was randomly assigned.

The RGE also used a split-plot design. Species were the split plots and 10 seedlings represented each species. Treatments were the whole plots with six replicates. A 21-degree pot angle was maintained to promote root growth along the clear sidewall of the PVC pots. To simulate flooding, tanks were filled with deionized water to a depth of 8 to 10 cm above the pot surface or 10–12 cm above the soil surface. Effects of extended and short flood seasons were contrasted for the RGE with the flood treatments (1) 1 October – 1 June, (2) 15 November – 15 February, and (3) a well-watered unflooded control. Species block positions were randomly assigned within each treatment by replication combination to reduce shading effects caused by inherent species growth differences..

The majority of the flooding in these treatments was during the 'dormant season', when floodwaters are most likely to remain on bottomland hardwoods forests in the southeastern US (Wigley and Filer, 1989; Young et al., 1995). In this study, measurements began in the fall just prior to flood treatment implementation and continued through the end of September the following fall. Measurements presented include survival, height, root elongation, and presence or absence of black roots. Root measurements and inspections were

transferred to clear acetate sheets on a weekly basis. The acetate sheets were scanned and the images were measured with the GS Root Program (PP Systems, Havervill Massachusetts). Image lengths were calibrated against scanned wire images of known lengths, similar in magnitude to the root system being scanned.

Analyses

In the field study, data were tested for homogeneity of variance using the Hartley test. When variances proved heterogeneous, data were transformed until variance became homogeneous (according to Burke et al., 1992) before statistics were performed. Basic statistics and '*t*'-tests were performed using the GLM procedure, means statement, and *t* options of SAS (SAS, 1985). Confidence intervals for the water level regressions were calculated using the residual mean squares from the ANOVA according to Steele and Torrie (1960).

For the SGE and RGE experiments, analysis of variance by GLM (General Linear Models) was used to compare least square means, with probability level set at a <0.05. Seedling survival was quantified near the beginning (May 15) and end (September 30) of the growing season. Since survival was categorical, arc-sine transformations of the least square means were used in the statistical analysis. The GML procedure of the Statistical Analysis System (SAS) was used for that analysis. Survival was presented as retransformed data for comparison purposes.

Results

Ecosystem study

Hydrologic characterization
Regression models predicted that the swamp tupelo and laurel oak forest types were inundated 61 and 3% of the time, respectively, and were saturated within 30 cm of the surface 84% and 20% of the time, respectively. Depth to the water table exceeded 1 m each summer in the laurel oak community, but only rarely did it drop below 30 cm in the swamp tupelo type (Figure 1).

Ecosystem root dynamics
The first sample of root biomass revealed that 98 and 96% of fine root biomass occurred in the upper 45 cm of the surface 60 cm soil profile for the swamp tu-
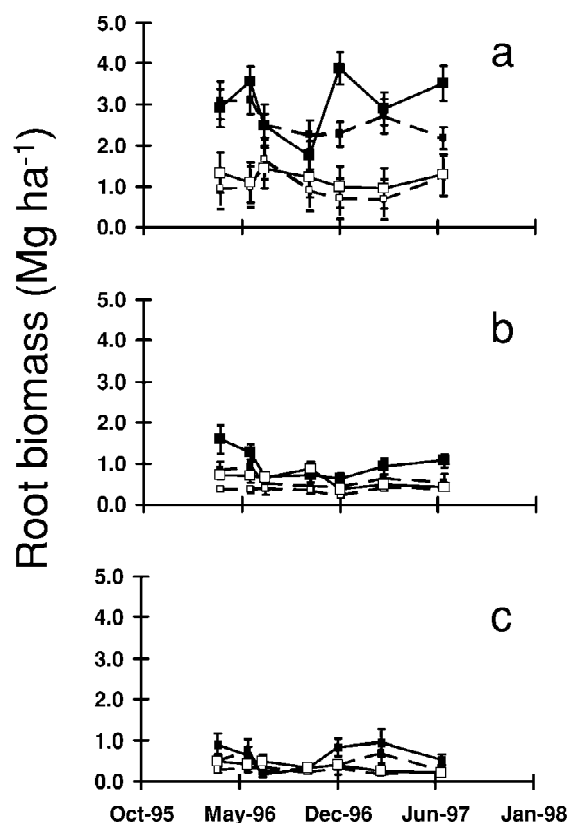

Figure 2. Mean (± SE) fine root biomass in the laurel oak (black symbol) and swamp tupelo (white symbol) habitats for roots < 1 mm diameter (small square) and 1–3 mm diameter (large square) in soil depth intervals (a) 0–15 cm, (b) 15–30 cm, and (c) 30–45 cm (*n* = 15).

pelo and laurel oak habitats, respectively. As a result, subsequent sampling was limited to 45 cm soil depths.

Fine root biomass was greater in the laurel oak forest type (5.7 Mg ha^{-1}) than in the swamp tupelo type (2.4 Mg ha^{-1}), and this difference was most pronounced at the 0–15 cm depth interval. In the swamp tupelo type, root mass declined less dramatically with depth. In the laurel oak type, roots 1–3 mm diameter comprised most of the fine root biomass, and these roots were more dynamic (greater increase and decrease in mass over time) than were the smaller diameter roots (Figure 2). In the swamp tupelo habitat, biomass was similar among root diameter size classes, and it was the smaller roots that were more dynamic. The phenology of root production differed between forest types. In the laurel oak habitat, root production occurred mainly during the fall in the surface 15 cm depth. In summer, root biomass declined sharply at this depth in that habitat. In the swamp tu-
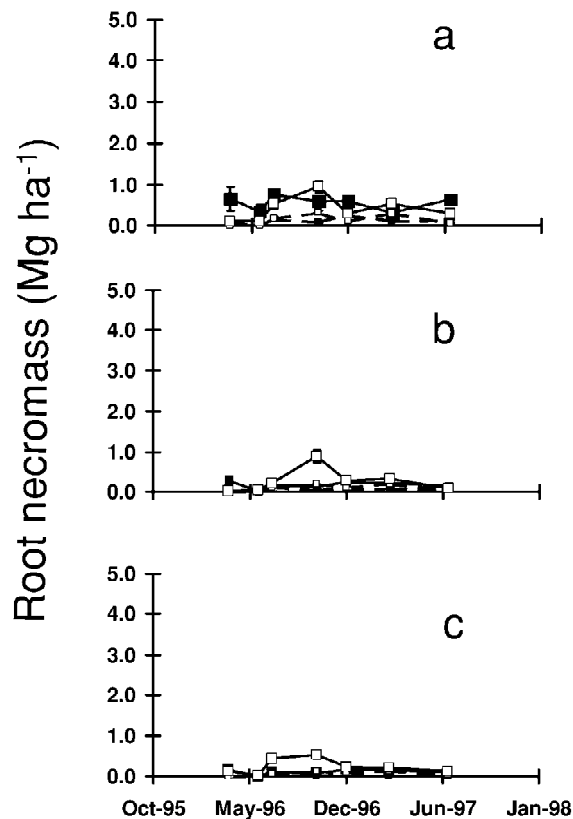
Figure 3. Mean (± SE) fine root necromass in the laurel oak and swamp tupelo habitats. Designations are given in caption to Figure 2 (*n* = 15).
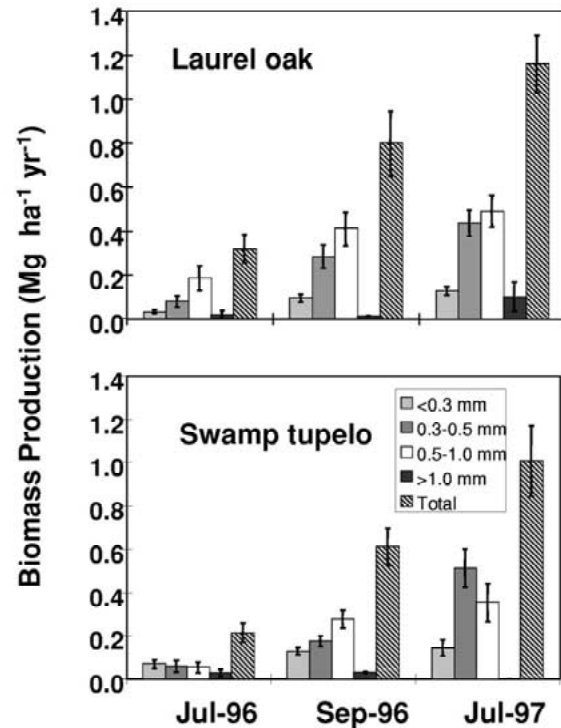

Figure 4. Mean (± SE) root biomass production by diameter size class estimated using intersections of new roots with fiberglass screen inserted into soil at a 45 degree angle to a soil depth of 15 cm.

pelo community, only the smallest diameter roots had measurable production during the spring in the upper 15 cm soil depth. Biomass of larger diameter roots and roots in the deeper soil did not vary. As a result, production estimates between April 1996 and March 1997 were 2.3 Mg ha^{-1} yr^{-1} for laurel oak and 0.3 Mg ha^{-1} yr^{-1} for swamp tupelo habitats when the sum of significant increments method was used, and 5.6 and 2.5 Mg ha $^{-1}$ yr^{-1}, respectively when the maximum minus minimum method was used.

In contrast to biomass, fine root necromass (2.4 Mg ha^{-1} laurel oak and 1.3 Mg ha^{-1} for swamp tupelo) was similar among depths and between forest types (Figure 3). Regardless of whether mortality was calculated using the sum of significant increments or the maximum minus minimum methods, mortality was lower in the laurel oak habitat (1.3 and 1.2 Mg ha^{-1} yr^{-1}) than in the swamp tupelo community (2.8 and 2.1 Mg ha^{-1} yr^{-1}), apparently a contradiction when changes in biomass and productivity are considered.

When the root screen method was used, production was 1.2 (±0.1 SE) Mg ha^{-1} yr^{-1} for laurel oak and 1.0 (±0.2 SE) Mg ha^{-1} yr^{-1} for the swamp tupelo forest type. Roots 0.3–0.5 mm diameter were most important for biomass production in the swamp tupelo forest type and roots 0.3–1.0 mm diameter were most important in the laurel oak type (Figure 4).

Root length production was 9510 km ha^{-1} yr^{-1} for laurel oak and 10 950 km ha^{-1} yr^{-1} for the swamp tupelo forest types, with roots < 0.3 mm most productive in the laurel oak habitat and roots <0.3 and 0.3–0.5 mm equally productive in the swamp tupelo habitat (Figure 5). Root surface area production was 1.2 ha ha^{-1} yr^{-1} for laurel oak and 1.4 ha ha^{-1} yr^{-1} for swamp tupelo habitats.

Seedling study

Differences in seedling mortality among oak species were observed in only the weeks after pots were drained. Cherrybark and swamp chestnut oaks had greater post-flooding mortality than overcup and water

Table 1. Percent survival (May 15 and September 30) of bottomland oak seedlings subjected to different flood duration and season[a]

Flood Regime	Swamp Chestnut Oak		Cherrybark		Water Oak		Overcup Oak	
	May 15	September 30	May 15	September 30	May 14	September 30	May 15	September 30
Control	94.6	80.6 A	99.0	91.6 A	100	99.1 A	100	96.1 A
Oct.15/May1	81.0	62.9 B	89.0	70.2 B	99.8	97.9 A	100	98.2 A
Oct 1/June1	70.4	22.1 C	92.0	/40.2 C	99.1	84.8 B	99.8	98.9 A

[a] Means within species followed by the same letter are not significantly different ($\alpha \leq 0.05$) for the September 30 date. Data are retransformed from arcsine transformed least square means and only represent relative differences.
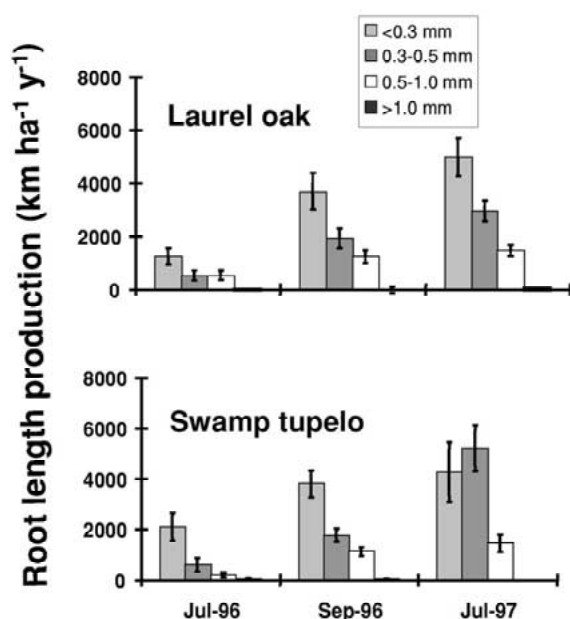

Figure 5. Mean ($\pm$ SE) root length production by diameter size class estimated using root ingrowth screens as explained in caption to Figure 4.

Table 2. Final least square mean height growth ratios [a] (and probabilities) as affected by flood treatment period

Species	Flood Period	
	Oct. 1-June1	Oct. 15-May 1
Cherrybark oak	0.10 (0.005)	0.40 (0.014)
Swamp Chestnut oak	0.10 (0.01)	0.28 (0.004)
Water oak	0.39 (0.005)	0.81 (ns)
Overcup oak	1.17 (ns)	1.05 (ns)

[a] Seedling height growth increment for each flood treatment period divided by height growth increment of the unflooded control seedlings during the same period for the same species.

flood treatments divided by root elongation of the respective control. 'No effect' resulted in index values of one, while values lower than one indicated a negative effect of flooding. Water oak and especially overcup oak had index values equal to or greater than one (Figure 6), suggesting that flooding enhanced or at least did not negatively influence root elongation in those species. In contrast, very low index values for cherrybark oak and swamp chestnut oak showed flooding seriously impacted root growth in those species. Under control conditions, root growth began relatively early for cherrybark oak, where 45% of growth occurred before June 1 in the control and was minimal after that date. In contrast, root growth in overcup oak occurred later, with only 25–30% occurring before June 1 in the control. As a result, root growth in overcup oak seedlings after June 1 was not influenced by flooding.

Black root tips, coatings of oxide precipitates of Mn and Fe, occurred in all species for both flooding treatments after draining. Frequency was greatest for cherrybark and swamp chestnut oaks, was intermediate for water oak, and only a few overcup oak seedlings developed black roots (Figures 7a, and b). Also, overcup oak was the species best able to re-
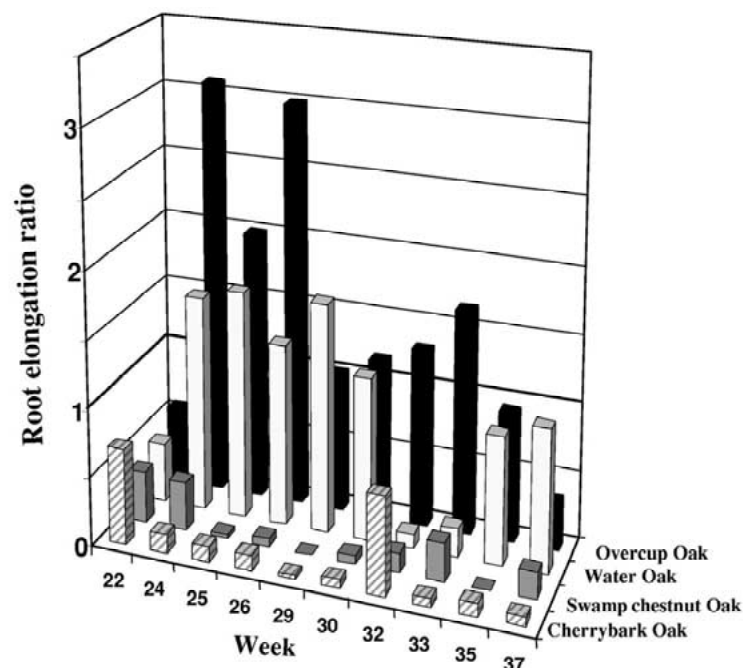
oaks, and mortality increased in those former species with the duration of flooding (Table 1).

Both flood treatments reduced stem height growth for cherrybark and swamp chestnut oaks, but growth for overcup oak was not affected by either flooding treatment. Growth for water oak was significantly reduced only by the longest flooding treatment (Table 2).

Similarly, there was a significant species/treatment interaction for root elongation. Growth responses ranged from no difference among treatments for overcup oak to dramatic reductions after flooding for cherrybark oak. We developed an index for flooding impact using the ratio of root elongation estimated in

Figure 6. Index of flooding impact using a ratio of values for root elongation for flood treatment over those for the control in weeks following flooding between October 15 and May 1.

cover from flooding, indicated by a disappearance of black color on roots by July 24 in most overcup oak seedlings.

Discussion

Fine root biomass, production, and turnover was greater in the laurel oak forest type, which also tended to have longer periods of aerated soil. We found extended periods of inundation were associated with lower root production, greater root longevity, a more abbreviated season during which roots were produced, and thinner roots, but not with a difference in the surface area of fine roots. These differences among vegetation types are attributed to species differences changes along hydrologic gradients and variations in soil properties including moisture availability, hypoxia, physical restriction of vertical root growth, and nutrient availability.

These findings support most of the previously published results for floodplain forests in the Southeastern United States (Table 3). However, there is one exception: our root biomass estimates were substantially greater than those of Baker et al., (2001) from an-

other part of the same study site. As a result, root turnover estimates based on Baker et al.'s root biomass values were high and may have been influenced by methodological differences (Pers. Comm. T. T. Baker, III).

There appeared to be a smaller investment of photosynthate to roots in the swamp tupelo versus the laurel oak habitat but there appeared to be similar absorptive capacity, due to a smaller mass but thinner roots in the swamp tupelo forest type. This assumes root surface area represents absorptive function, as was suggested by Rendig and Taylor (1989), and that production accurately represents photosynthate investment. In contrast, others (Baker et al., 2001) have suggested investment to roots was greater in a poorly drained site than a well-drained site, but they did not consider root diameter when calculating their root length to biomass conversion equations.

Root production estimates were expected to vary among methods (e.g. Burke and Raynal, 1994) due to inherent differences in assumptions among the methods. Knowledge of root dynamics is enhanced when results of several methods are compared (Vogt et al., 1998), because each method may best describe a different aspect of the complicated root turnover process.
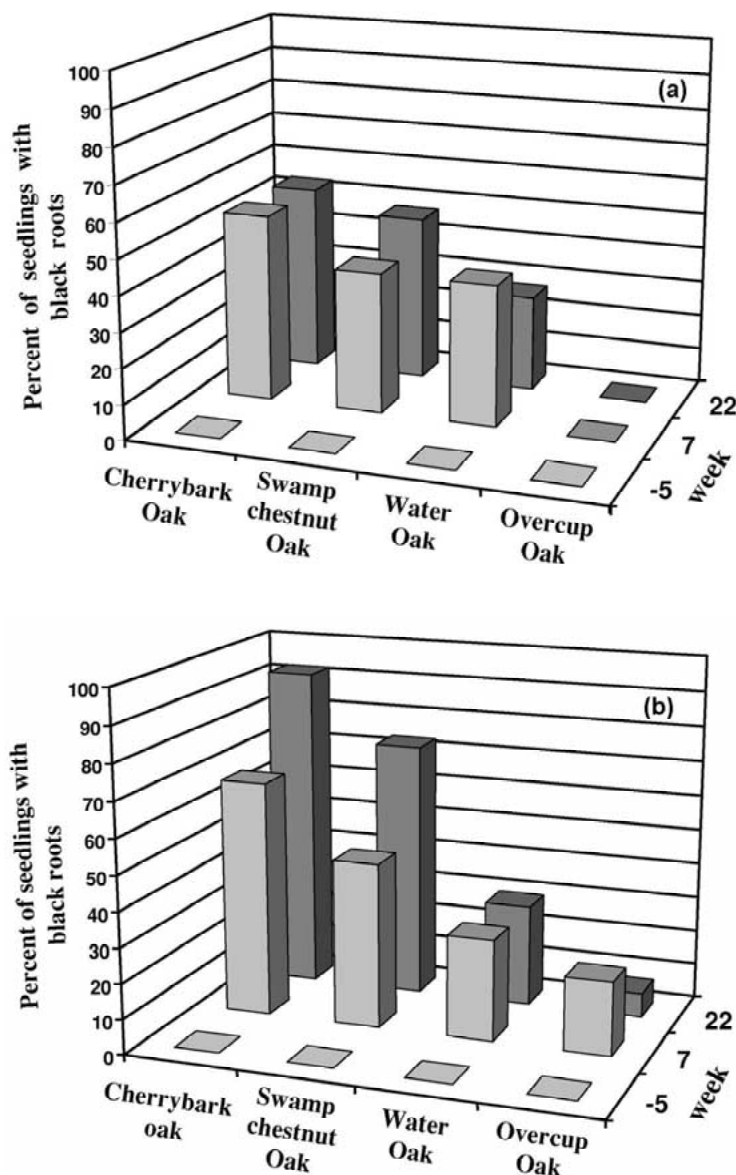
Figure 7. Proportion of seedlings with black roots present during the course of the experiment with flooding from October 15 to May 1 (a) and from October 1 to June 1 (b). Week '0' is end of flooding, week '–5' is five weeks prior to the end of flooding.

Also, because a variety of methods have been used in previous studies of root production, cross-study comparisons are more easily made when several methods can be compared within a study. Our estimates from the different approaches suggest one or more of the following scenarios is true: (1) root production was similar between habitats but mortality was greater and more continuous in the swamp tupelo habitat, causing us to underestimate production and mortality in the swamp tupelo forest type, (2) root production and mortality were greater in the laurel oak habitat, but because there was a greater proportion of roots thicker than the screen mesh, proportionally fewer roots were detected in the laurel oak habitat than in the swamp tupelo habitat when the screen method was used, (3) differences in sample integrity caused fewer roots to be overlooked in screens taken from the swamp tupelo compared to the laurel oak habitat, or (4) severing

Table 3. Fine root biomass, production, and turnover for Southeastern United States floodplain forests

Habitat	Fine root biomass (Mg/ha)	Fine root production (Mg/ha/y)	Rine root turnover[e]
Atlantic White Cedar[a]	5.0	2.7	54%
Baldcypress[a]	2.3	0.7	30%
Maple Gum[a]	2.4	0.6	25%
Mixed Hardwoods[a]	7.9	3.5	44%
Bottomland hardwood[b]	4.1	nd	nd
Well Drained[c]	1.0	1.5–2.1	150%–210%
Intermediately drained[c]	0.7	1.8	258%
Poorly Drained[c]	0.6	0.9–1.9	320%
Laurel Oak[d]	5.7	2.3	40%
Swamp Tupelo[d]	2.4	0.3	12%

[a]From Powell and Day (1991) for fine roots $\leq$ 2 mm diameter.
[b]From Farrish (1991), production and turnover values not available.
[c] From Baker et al. (2001) for fine roots $\leq$ 3 mm. [d] This study, for roots $\leq$ 3 mm, sum of significant increment method used for estimating root production. [e] Calculated as annual fine root production/fine root biomass.

roots during screen insertion stimulated root growth in the swamp tupelo forest type more than in the laurel oak forest type.

We believe the second scenario is the most plausible because larger roots (1–3 mm diameter) were more dynamic (more production and mortality) than smaller roots in the laurel oak habitat, and smaller roots were more dynamic than larger roots in the swamp tupelo habitat. Our turnover values were similar to what had been reported previously for floodplain forests in the Southeastern United States (Table 3) and are in agreement with Gill and Jackson's (2000) conclusion that root turnover in forested wetlands should be about $\frac{1}{2}$ of root biomass. Although fluctuations of root biomass in the laurel oak forest type were substantially greater than in the swamp tupelo type, an influx of dead root material was not detected in the pools of necromass in the former type, suggesting that either our estimates of mortality were inaccurate, or decomposition of the dead roots was more rapid in the laurel oak relative to the swamp tupelo habitat. In fact, roots of the laurel oak forest type were expected to have higher decomposition rates

than the more anaerobic swamp tupelo type. Even if dead root material in the laurel oak habitat was not more thoroughly decomposed, it may have been more fragmented and therefore more readily classified as detritus instead of as dead roots during sample processing. Material was classified as necromass only when it was clearly identified as dead roots. We documented a unimodal peak in production during the fall and a unimodal period of mortality during the summer in the laurel oak forest type. In the swamp tupelo type, we documented few changes in biomass or necromass through the year, and thus turnover values were low.

Although biomass estimates were quite different in this and Baker et al.,'s (2001) study, our production estimates were remarkably similar. For example, Baker et al.'s estimates for root production using the screen ingrowth method ranged from 1.8 Mg ha^{-1} yr^{-1} to 0.8 Mg ha^{-1} yr^{-1}, compared to our estimates of 1.2 and 1.0 Mg ha^{-1} yr^{-1}. Baker et al., sampled their screens more frequently than we did, but did not account for differences in diameters of roots intersecting the screens. We believe root diameter is important to consider, because we showed that root dynamics differed among root diameter categories within and between forest types. We believe the small mesh of the ingrowth screen may have selected against the thicker roots of the laurel oak type and hence underestimated root production for the laurel oak site. We concluded that underestimation of laurel oak production using the screen method was a possible reason that production estimates between habitats were similar when the screen method was used. Quite different values resulted when biomass differences were used to estimate fine root production.

Both floods and droughts are common on this floodplain (Burke et al., 2000a) and this extreme hydroperiod probably influenced root dynamics. Although differences in elevation were only about 20 cm, hydrologic regimes were quite different in the two habitats we studied (Eisenbies and Hughes, 2000). Drought was probably not important in the swamp tupelo habitat because soil was almost always saturated within 30 cm of the surface. However, post anoxic injury to roots may have occurred there, damage caused by free radical damage to tissues after flooding (Crawford, 1993). In the laurel oak community, the combination of summer drought and a restricted rooting depth probably caused substantial fine root mortality and turnover in that season, but provided conditions more conducive to growth during

cooler and wetter months. In fact, root biomass values support this conclusion.

Eissenstat et al. (2000) cautioned that it is premature to draw conclusions about relationships between root diameter, tissue density, or specific root length as predictors of root longevity, and instead recommended that predictions should be based on a cost benefit analysis: optimal life spans should be greater if construction costs are high relative to maintenance and uptake costs. In the swamp tupelo forest, consistently moist soil probably minimizes root maintenance and uptake costs, so roots are expected to be longer-lived there than those in the laurel oak type. In the latter forest type, frequent and extreme changes in soil moisture probably causes high root maintenance and uptake costs, and may make mortality and subsequent reconstruction of root systems the more energetically economical strategy. Large diameter roots are more energetically expensive to produce than are roots of small diameter (Caldwell, 1987), but large roots can be more effective in moisture transport. Absorption is more directly related to root length and surface area than biomass, other things being equal (Rendig and Taylor, 1989), so root function is probably best quantified in units of length or surface area although investment is best quantified in units of mass. The laurel oak forest type had larger diameter roots on average, yet root length and surface area were similar between the forest types. Also, thicker fine roots were more dynamic than very fine roots in the laurel oak habitat, and a greater amount of those roots were eliminated during the summer drought period. This suggested that similar root function was maintained in the two habitats with quite different investment strategies. There appeared to be a great investment to roots in the laurel oak habitat, although this high turnover may have been less costly to trees than maintaining non-functional root biomass through the summer drought. In contrast, small diameter roots are less expensive to produce (and probably maintain), so production and maintenance of small roots may be advantageous when conditions are less extreme, such as in the swamp tupelo habitat. As a result, either root production and mortality were small but continuous or roots were relatively long-lived in the swamp tupelo habitat.

Because trees tend to allocate carbon to maximize benefits gained relative to investment (Eissenstat, 1997), responses to environmental differences may help explain species-specific strategies. To date, growth responses of trees to different hydroperiods have focused on aboveground components, although

an ability to maintain sink strength in root tissue under flooded conditions has been linked to flood tolerance (Angelov et al., 1996). Also, flood tolerance was associated with the ability to produce new 'water roots' when flooded (Hook and Brown 1973). Sweetgum and swamp tupelo are effective at 'turning over' their roots and improving root function when flooded (Angelov et al., 1996; Hook and Brown, 1973; Hook et al., 1971). Trees that cannot make these changes tend to be intolerant to flooding. At least theoretically, floodplains in the southern United States should support trees that can produce new roots as the water levels change because intermittent flooding and draining is characteristic of these systems (Hupp, 2000). It follows that root turnover under those conditions should be greater than in either continually flooded swamps or drained mesic sites.

Several species of oak are found in the floodplains of the Atlantic Coastal Plain, including laurel oak (McReynold and Hebb, 1990), overcup oak (Vozzo, 1990), and water oak (Solomon, 1990) in the most flood prone habitats. Also, swamp chestnut oak is found in moist bottomlands (Edwards, 1990) and cherrybark oak is found on loamy sites on first bottom ridges and well-drained terraces (Krinard, 1990). The floodplain oaks tend to remain vigorous when flooded although declines in root function have been documented during and after flooding (Angelov et al., 1996; Harms et al., 1980). We found roots of the most flood tolerant, overcup oak (1) were not affected or were positively affected by flooding episodes in the dormant season, (2) remained dormant until flood water receded, and (3) experienced low root tip mortality and when flooding caused mortality there was quick recovery. In contrast, cherrybark and swamp chestnut oak had substantial mortality and did not recover after flooding, an indication that those species were not able to aerate their rhizosphere like the flood tolerant trees (Levan and Riha, 1986).

Flood tolerant trees are known to maintain sink strength in their roots under flooded conditions (Angelov et al., 1996), and we observed vigorous root growth for both overcup and water oaks in flood treatments, sometimes exceeding growth in the control. Reductions in root growth after flooding for cherrybark and swamp chestnut oaks supported previous reports for these species where survival, aboveground growth, and photosynthetic ability declined (Angelov et al., 1996).

Overcup oak had a notable strategy for maximizing benefit while minimizing costs; an abbreviated

season of root growth that avoided seasons with high probability of flooding. This strategy may help explain why flooding actually stimulates growth on some sites (Broadfoot, 1967; Fredrickson, 1978). However, that same characteristic that provided flood tolerance could limit the success of overcup oak on better drained sites where trees with longer seasons of root growth could out-complete flood tolerant trees for soil resources. The experimental results identified contrasting root growth strategies that help explain the basis of flood tolerance and differences in root dynamics in different bottomland hardwood forest types.

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